Merino ewes can be bred for body weight change to be more tolerant to uncertain feed supply[1]

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ABSTRACT: Sheep in Australia experience periods with different feed supply causing them to gain and lose BW during the year. It is more efficient if ewes lose less BW during periods of poor nutrition and gain more BW during periods of good nutrition. We investigated whether BW loss during periods of poor nutrition and BW gain during periods of good nutrition are genetically different traits. We used BW measurements from 2,336 adult Merino ewes managed over 5 yr in a Mediterranean climate in Katanning, Australia. Body weight loss is the difference between 2 BW measured 42 d apart during mating, a period of poor nutrition. Body weight gain is the difference between 2 BW measured 131 d apart during a period of good nutrition between prelambing and weaning. We estimated variance compnents of BW change using 3 methods: 1) as a trait calculated by subtracting the first BW from the second, 2) multivariate analysis of BW traits, and 3) random regression analysis of BW. The h^2 and genetic correlations (r_g) estimated using the multivariate analysis of BW and the BW change trait were very similar whereas the random regression analysis estimated lower heritabilities and more extreme negative genetic correlations between BW loss and gain. The multivariate model fitted the data better than random regression based on Akaike and Bayesian information criterion so we considered the results of the multivariate model to be more reliable. The heritability of BW loss (h^2 = 0.05–0.16) was smaller than that of BW gain (h^2 = 0.14–0.37). Body weight loss and gain can be bred for independently at 2 and 4 yr of age (r_g = 0.03 and –0.04) whereas at 3 yr of age ewes that genetically lost more BW gained more BW (r_g = –0.41). Body weight loss is genetically not the same trait at different ages (r_g range 0.13–0.39). Body weight gain at age 3 yr is genetically the same trait at age 4 yr (r_g = 0.99) but is different between age 2 yr and the older ages (r_g = 0.53 and 0.51). These results suggest that as the ewes reach their mature BW, BW gain at different ages becomes the same trait. This does not apply to BW loss. We conclude that BW change could be included in breeding programs to breed adult Merino ewes that are more tolerant to variation in feed supply.

Key words: breeding, climate change, heritability, body weight change, sheep

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INTRODUCTION

The wool and lamb industry in Australia is mostly in the Mediterranean climate regions of southern Australia, using mostly Merino ewes. The rainfall patterns of these regions are expected to be more variable and less winter dominant (IPCC, 2007) with the length and severity of the annual periods of drought harder to predict. This erratic climate will make managing

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sheep more difficult as most Merino ewes lose BW during summer and autumn and then regain BW during late winter and spring (Adams and Briegel, 1998). Farmers currently overcome some of the deficit in pasture feed by feeding grain, hay, or silage but this has major feed and labor costs (Young et al., 2011b).

A possible solution is to breed sheep that can maintain BW during times of feed shortage and are therefore more resilient to variation in feed supply. Borg et al. (2009) and Rauw et al. (2010) estimated moderate heritabilities for BW loss and gain in adult ewes grazing in rangelands. However, these studies did not investigate if BW change is genetically different between periods of poor and good nutrition. They also did not compare BW change in younger ewes to older ewes, which could be genetically different traits.

Also, heritability of BW change can be calculated using the variance of each BW measurement and the covariance between them. These variances can be estimated treating each BW measurement as an individual trait in a multivariate analysis or treating BW as a repeated measure over time in a random regression model (Van der Werf et al., 1998).

In this study we tested the hypothesis that BW loss during summer and BW gain during pasture growth are different traits. We also tested the hypothesis that BW change is a different trait in young ewes compared with mature ewes. We tested these hypotheses using 3 methods: BW change traits, random regression analysis, and multivariate analysis.

MATERIALS AND METHODS

The management of the ewes was approved by the Animal Ethics and Welfare Committee from the Department of Agriculture, Western Australia. More details about how the ewes were managed are in Greeff and Cox (2006).

Animals and their Management

We used BW information from 2,336 fully pedigreed adult ewes from the Merino Resource flocks of the Department of Agriculture and Food Western Australia at Katanning (33°41′ S, 117°35′ E, and elevation 310 m). Katanning is in the Mediterranean climate region with hot dry summers and mild wet winters. This combination of temperature and rainfall means there is a period when pasture does not grow during summer and autumn. All ewes were managed on 1 farm under conditions typical for commercial farms in that area. The ewes were fed two-thirds lupins and one-third oats. The amount fed varied between years but on average ewes were fed 100 g per animal per day in late December increasing gradually to 800 g per head per day at lambing. Hay was fed ad libitum during lambing. Lambing time was in July and ewes were shorn in October when the weight of greasy wool was recorded.

Table 1. Timing of 4 BW recordings in Katanning Resource Flock from 2000 to 2005

	Traits[1]			
Year	WT1	WT2	WT3	WT4
2000	10 Jan.	23 Feb.	30 May	27 Sept.
2001	16 Jan.	23 Feb.	6 May	25 Sept.
2002	15 Jan.	26 Feb.	3 June	8 Oct.
2003	13 Jan.	26 Feb.	3 June	7 Oct.
2004	13 Jan.	23 Feb.	17 May	7 Oct.
2005	11 Jan.	25 Feb.	18 May	3 Oct.
Average	13 Jan.	24 Feb.	23 May	2 Oct.
Avg days from start of year	13	55	143	274

[1]WT1 = premating BW; WT2 = postmating BW; WT3 = prelamb BW; WT4 = weaning BW.

Body Weight Data

We used BW recorded from years 2000 to 2005. Ewes were weighed 4 times annually at approximately the same time each year (Table 1). The 4 BW were premating BW (**WT1**), postmating BW (**WT2**), prelamb BW (**WT3**), and weaning BW (**WT4**). There were 898 ewes with 1 yr set, 715 with 2 yr sets, and 723 with 3 yr sets of all 4 BW, WT1, WT2, WT3, and WT4. There were 4,497 animal–age combinations of all 4 BW with on average 1.9 yr data per ewe of which 1,868 were for 2-yr-old ewes in their first parity, 1,501 for 3-yr-old ewes, and 1,128 for 4-yr-old ewes. The total pedigree file consisted of 29,300 sheep tracing back 10 generations, with 760 sires and 8,540 dams. One sire was mated with an average of 20 ewes with 1 paddock per sire.

We adjusted BW for wool weight, assuming constant wool growth during the year regardless of season and for conceptus weight using the equations from the GRAZPLAN model (Freer et al., 1997). We estimated conceptus weight using actual birth weight of the lambs instead of standard birth weight used by Freer et al. (1997). Over the 6 yr, 590 ewes gave birth to no lambs, 2,637 gave birth to 1 lamb, and 1,270 ewes gave birth to multiple lambs.

Genetic Analysis

To compare BW change at different times during the year and at different ages, we used 3 methods.

Body Weight Change Trait Analysis. The first BW was subtracted from the second BW to define a BW change trait such as in Borg et al. (2009) and Rauw et al. (2010). Then we estimated the variance components of the BW change traits at each age and the genetic correlations between ages (e.g., between young ewes and mature ewes).

Multivariate Analysis of BW. Here we used the BW at each time point as different traits in a multivariate analysis to estimate genetic variance for each BW and covariance between each BW point during the year within each age group. Subsequently, these estimates were used to calculate heritabilities and genetic correlations for BW loss and gain using variance and covariance rules.

Random Regression Analysis of BW. Here we used random regression to model changes in variances and covariances of BW within a year using continuous polynomial functions. This allows the genetic variance to be estimated for BW change between any days within a year.

Variance components were estimated using ASReml (Gilmour et al., 2006). We assumed convergence if REML log-likelihood changed less than 0.002 × the previous log-likelihood and the variance parameter estimates changed less than 1% over 6 runs. Goodness of fit of the multivariate and random regression analysis of BW was determined using the Akaike's information criterion (**AIC**; Akaike, 1973) and the Bayesian-Schwarz information criterion (**BIC**; Schwarz, 1978). It was not possible to compare these analyses that use 4 BW to the BW change trait analysis that uses 2 BW change traits.

Fixed Effects

We included fixed effects in all models for all traits for year (2000 to 2005), number of lambs born by each ewe in the year of BW measurement (0 to 2), number of lambs reared in the year of BW measurement (0 to 2), number of lambs born in the year before the BW measurements (0 to 2), and number of lambs weaned in the year before the BW measurements (0 to 2). In the random regression analyses we nested a fixed curve for average BW over time within these fixed effects.

Body Weight Change Trait Analysis

To analyze BW loss and gain as 2 separate traits, we defined BW loss (**LOSS**) as LOSS = WT2 – WT1 and BW gain (**GAIN**) as GAIN = WT4 – WT3.

This means that if LOSS or GAIN is negative, then the ewe lost BW, and if LOSS or GAIN is positive, then the ewe gained BW. The WT1 and WT2 were on average 42 d apart and recorded during a period of poor nutrition in January and February during mating. Body weights WT3 and WT4 were measured on average 131 d apart during a period of good nutrition period between May and October, during lactation.

We did multivariate analyses for LOSS and GAIN for ages 2, 3, and 4 yr. The model used for age-specific LOSS and GAIN was

$$\begin{bmatrix} y_{\text{age2}} \\ y_{\text{age3}} \\ y_{\text{age4}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{\text{age2}} & 0 & 0 \\ 0 & \mathbf{X}_{\text{age3}} & 0 \\ 0 & 0 & \mathbf{X}_{\text{age4}} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{\text{age2}} \\ \mathbf{b}_{\text{age3}} \\ \mathbf{b}_{\text{age4}} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{\text{age2}} & 0 & 0 \\ 0 & \mathbf{Z}_{\text{age3}} & 0 \\ 0 & 0 & \mathbf{Z}_{\text{age4}} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{\text{age2}} \\ \mathbf{a}_{\text{age3}} \\ \mathbf{a}_{\text{age4}} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{\text{age2}} \\ \mathbf{e}_{\text{age3}} \\ \mathbf{e}_{\text{age4}} \end{bmatrix},$$

in which y_{age2}, y_{age3}, and y_{age4} are the observations for LOSS or GAIN when ewes are 2, 3, and 4 yr old, $\mathbf{b}_i$ is the vector of fixed effects, $\mathbf{a}_i$ is the vector of additive genetic effects, $\mathbf{e}_i$ is the vector of error effects, and $\mathbf{X}_i$ and $\mathbf{Z}_i$ are the incidence matrices (i = age 2, age 3, and age4 yr).

$$\text{Var}\begin{bmatrix} \mathbf{e}_{\text{age2}} \\ \mathbf{e}_{\text{age3}} \\ \mathbf{e}_{\text{age4}} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I}$$

where

$$\mathbf{R} = \begin{bmatrix} \sigma^2_{\text{e age2}} & \text{cov}_{\text{e age2 age3}} & \text{cov}_{\text{e age2 age4}} \\ \text{cov}_{\text{e age3 age2}} & \sigma^2_{\text{e age3}} & \text{cov}_{\text{e age3 age4}} \\ \text{cov}_{\text{e age4 age2}} & \text{cov}_{\text{e age4 age3}} & \sigma^2_{\text{e age4}} \end{bmatrix}$$

and

$$\text{Var}\begin{bmatrix} \mathbf{a}_{\text{age2}} \\ \mathbf{a}_{\text{age3}} \\ \mathbf{a}_{\text{age4}} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A}$$

where

$$\mathbf{G} = \begin{bmatrix} \sigma^2_{\text{a age2}} & \text{cov}_{\text{a age2 age3}} & \text{cov}_{\text{a age2 age4}} \\ \text{cov}_{\text{a age3 age2}} & \sigma^2_{\text{a age3}} & \text{cov}_{\text{a age3 age4}} \\ \text{cov}_{\text{a age4 age2}} & \text{cov}_{\text{a age4 age3}} & \sigma^2_{\text{a age4}} \end{bmatrix},$$

in which **I** is the identity matrix, **A** is the additive genetic relationship matrix, and ⊗ is the direct matrix product operator.

We used bivariate analyses to estimate genetic correlations between each LOSS and GAIN at each age, similarly as between ages (Eq. [1]).

Multivariate Analysis of BW

We estimated the covariance or variancecomponents between the 4 BW measurements (WT1, WT2, WT3, and WT4) in each age group using a multivariate analysis:

$$\begin{bmatrix} y_{WT1} \\ y_{WT2} \\ y_{WT3} \\ y_{WT4} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{WT1} & 0 & 0 & 0 \\ 0 & \mathbf{X}_{WT2} & 0 & 0 \\ 0 & 0 & \mathbf{X}_{WT3} & 0 \\ 0 & 0 & 0 & \mathbf{X}_{WT4} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{WT1} \\ \mathbf{b}_{WT2} \\ \mathbf{b}_{WT3} \\ \mathbf{b}_{WT4} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{WT1} & 0 & 0 & 0 \\ 0 & \mathbf{Z}_{WT2} & 0 & 0 \\ 0 & 0 & \mathbf{Z}_{WT3} & 0 \\ 0 & 0 & 0 & \mathbf{Z}_{WT4} \end{bmatrix} \begin{bmatrix} \mathbf{a}_{WT1} \\ \mathbf{a}_{WT2} \\ \mathbf{a}_{WT3} \\ \mathbf{a}_{WT4} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{WT1} \\ \mathbf{e}_{WT2} \\ \mathbf{e}_{WT3} \\ \mathbf{e}_{WT4} \end{bmatrix},$$

in which y_{WT1}, y_{WT2}, y_{WT3}, and y_{WT4} are the observations for WT1, WT2, WT3, and WT4, $\mathbf{b}_i$ is the vector of fixed effects, $\mathbf{a}_i$ is the vector of additive genetic effects, $\mathbf{e}_i$ is the vector of residuals, and $\mathbf{X}_i$ and $\mathbf{Z}_i$ are the incidence matrices (i = WT1, WT2, WT3, and WT4).

$$\mathrm{Var}\begin{bmatrix} \mathbf{e}_{WT1} \\ \mathbf{e}_{WT2} \\ \mathbf{e}_{WT3} \\ \mathbf{e}_{WT4} \end{bmatrix} = \mathbf{R} \otimes \mathbf{I},$$

$$\mathbf{R} = \begin{bmatrix} \sigma^2_{e\,WT1} & cov_{e\,WT1\,WT2} & cov_{e\,WT1\,WT3} & cov_{e\,WT1\,WT4} \\ cov_{e\,WT2\,WT1} & \sigma^2_{e\,WT2} & cov_{e\,WT2\,WT3} & cov_{e\,WT2\,WT4} \\ cov_{e\,WT3\,WT1} & cov_{e\,WT3\,WT2} & \sigma^2_{e\,WT3} & cov_{e\,WT3\,WT4} \\ cov_{e\,WT4\,WT1} & cov_{e\,WT4\,WT2} & cov_{e\,WT4\,WT4} & \sigma^2_{e\,WT4} \end{bmatrix}$$

and

$$\mathrm{Var}\begin{bmatrix} \mathbf{a}_{WT1} \\ \mathbf{a}_{WT2} \\ \mathbf{a}_{WT3} \\ \mathbf{a}_{WT4} \end{bmatrix} = \mathbf{G} \otimes \mathbf{A},$$

$$\mathbf{G} = \begin{bmatrix} \sigma^2_{a\,WT1} & cov_{a\,WT1\,WT2} & cov_{a\,WT1\,WT3} & cov_{a\,WT1\,WT4} \\ cov_{a\,WT2\,WT1} & \sigma^2_{a\,WT2} & cov_{a\,WT2\,WT3} & cov_{a\,WT2\,WT4} \\ cov_{a\,WT3\,WT1} & cov_{a\,WT3\,WT2} & \sigma^2_{a\,WT3} & cov_{a\,WT3\,WT4} \\ cov_{a\,WT4\,WT1} & cov_{a\,WT4\,WT2} & cov_{a\,WT4\,WT4} & \sigma^2_{a\,WT4} \end{bmatrix},$$

in which **I** is the identity matrix and **A** is the relationship matrix.

Calculation of Genetic Parameters Using Multivariate Analysis of BW

We estimated the additive genetic and residual variance for LOSS and GAIN using the variances of the 2 involved BW and the covariance between them. For example, the additive genetic variance for LOSS (WT2 – WT1) was calculated using

$$\sigma^2_{a\,(WT2-WT1)} = \sigma^2_{a\,WT2} + \sigma^2_{a\,WT1} - 2 \times cov_a(WT2,WT1),$$

in which $\sigma^2_{a\,WT2}$ and $\sigma^2_{a\,WT1}$ are the additive genetic variances of WT1 and WT2, respectively, and cov_a(WT2,WT1) is the additive genetic covariance between WT2 and WT1. This means that when the covariance between BW points is positive, variance in BW change exists only when twice the covariance between 2 points is lower than the variance of the 2 points. This means highly correlated points will have less variance for the BW change between them.

We calculated the genetic covariance between LOSS (WT2 – WT1) and GAIN (WT4 – WT3) using

$$cov_a(WT2-WT1, WT4-WT3) = cov_a(WT2, WT4) - cov_a(WT2, WT3) - cov_a(WT1, WT4) + cov_a(WT1,WT3),$$

in which cov_a is the additive genetic covariance between BW at each measurement time indicated in the parentheses.

Random Regression Analysis of BW

We used random regression to analyze BW change as a continuous function of time across the seasons (Henderson, 1982; Schaeffer, 2004). This random regression analysis was done separately for ages 2, 3, and 4 yr.

$$\mathbf{Y} = \mathbf{X}b + \boldsymbol{\theta}_{\mathbf{a}}k_a + \boldsymbol{\theta}_{\mathbf{p}}k_p + e,$$

in which **Y** is a vector of observations for BW of individual ewes, **X** is the incidence matrix for the vector of the fixed effects b, $\boldsymbol{\theta}_{\mathbf{a}}$ and $\boldsymbol{\theta}_{\mathbf{p}}$ are the matrices with orthogonal polynomial coefficients of $j \times i$ dimensions in which j is the number of polynomial coefficients and i is the number of BW points standardized to the first and last time points. Matrices $\boldsymbol{\theta}_{\mathbf{a}}$ and $\boldsymbol{\theta}_{\mathbf{p}}$ correspond to additive genetic and permanent environmental with random regression coefficients k_a and k_p, and e is the random residual. Permanent environmental effects were estimated to account for nongenetic effects common to repeated BW measurements.

We fitted the fixed curve of average BW as a third order polynomial nested within year, number of lambs born by each ewe in the year of BW measurement (0 to 2), number of lambs reared in the year of BW measurement (0 to 2), number of lambs born in the year before the BW measurements (0 to 2), and number of lambs weaned in the year before the BW measurements (0 to 2). The third order was the greatest possible order using 4 data points and was the best fit based on F-tests. We then selected the order of fit for the random effects, additive genetic and permanent environmental, by comparing the 9 possible models for each age from order 1 to 3. The best fit of the 9 different models was based on the BIC. The optimum fit for all ages was the third order for additive genetic effects and the first order for permanent environmental effects.

We included 4 separate residual variance classes along the time x axis, 1 for each time point, because the residual variance for each separate BW measurement estimated using the multivariate analysis was different. Due to the small variation in measurement date between years, these classes were 10 to 16, 54 to 57, 126 to 154, and 268 to 281 d from the start of the year. We used these 4 time points because it maximized the number of individuals that could be included in the analysis as most ewes were culled between weaning and the next mating, so most ewes had BW for the first 4 BW of the year.

The variances and covariances between the 4 BW points were calculated based on the random regression variance–covariance functions at 13, 55, 143, and 274 d from the start of the year.

The additive genetic variance and permanent environmental variance and covariance between LOSS and GAIN were calculated using the same equations as in the multivariate analysis of BW analysis. The only difference was that the phenotypic variance for LOSS and GAIN was estimated by adding the additive genetic and permanent environmental variances estimated from the random curves to the estimates for residual variance at the relevant time points. These residual estimates were assumed to be independent of each other because we estimated the permanent environmental effects to account for environmental covariances between time points.

RESULTS

As ewes aged they got heavier and their BW varied less over the year (Table 2). The ewes were lighter at age 2 yr at each point in the year and ewes aged 4 yr were the heaviest. Additionally, the ewes on average lost BW between WT1 and WT2 (LOSS) and gained BW between WT3 and WT4 (GAIN) at all ages with younger ewes (age 2 yr) losing and gaining more BW than older ewes (age 3 yr and age 4 yr). This suggests that ewes aged 2 yr were still growing to maturity.

Variance of BW

The additive genetic variance of BW was mostly similar when estimated using multivariate analysis of BW and random regression (Fig. 1). At age 3 yr the additive variance of BW estimated using random regression as compared with multivariate analysis was greater for WT1 and WT2 and lower for WT4. The additive variance at age 4 yr was greater for WT3 and lower for WT4 when estimated with random regression compared with multivariate analysis of BW. We used these variances and the covariance between each BW measurement to estimate the heritability of BW change.

Additive Genetic Variance, Phenotypic Variance, and Heritability Estimates for BW loss

The multivariate analysis of BW fit the data better than random regression at all ages according to the BIC and AIC (Table 3). Table 4 shows estimates of the variance components for LOSS using the variance and covariance estimated with random regression and multivariate analyses of BW. The additive variance for LOSS was greater using multivariate whereas residual variance was greater using random regression. The heritability of

Table 2. Mean and SD of BW 1 to 4, BW loss (LOSS) and BW gain (GAIN) of ewes aged 2, 3, and 4 yr old

Trait[1]	Mean, kg	SD, kg
WT1 age = 2 yr	50.2	6.24
WT1 age = 3 yr	58.6	7.09
WT1 age = 4 yr	61.7	7.30
WT2 age = 2 yr	48.0	6.46
WT2 age = 3 yr	58.0	6.45
WT2 age = 4 yr	60.7	6.62
WT3 age = 2 yr	50.3	6.04
WT3 age = 3 yr	58.5	6.77
WT3 age = 4 yr	60.9	7.13
WT4 age = 2 yr	56.9	7.41
WT4 age = 3 yr	61.7	8.13
WT4 age = 4 yr	63.7	8.70
LOSS age = 2 yr	–2.23	2.73
LOSS age = 3 yr	–0.606	3.95
LOSS age = 4 yr	–0.968	3.79
GAIN age = 2 yr	6.55	7.20
GAIN age = 3 yr	3.14	7.20
GAIN age = 4 yr	2.83	7.41

[1]WT1 = premating BW; WT2 = postmating BW; WT3 = prelamb BW; WT4 = weaning BW.

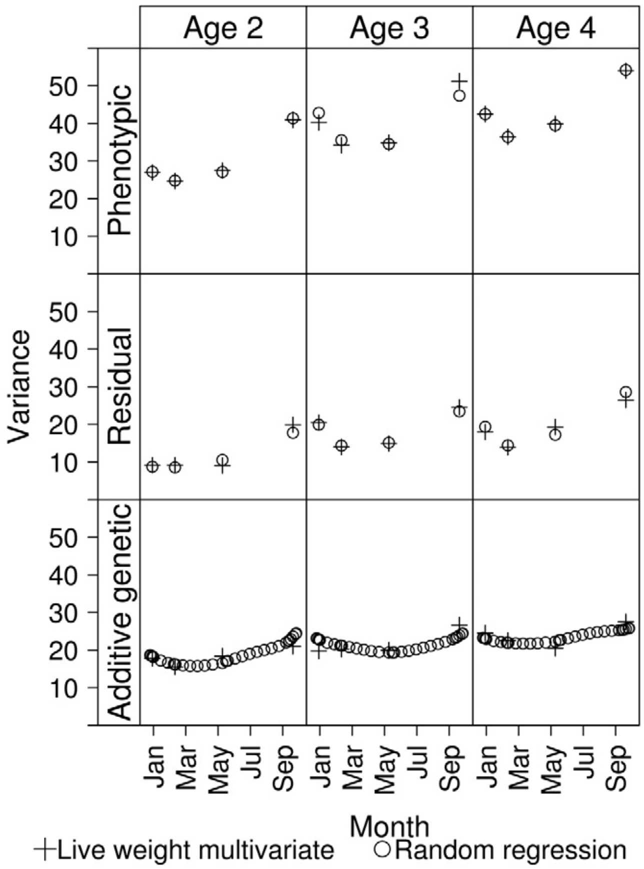

Figure 1. Variance components for BW estimated using multivariate analysis of BW and random regression analysis with third order polynomial for additive genetic variance and first order polynomial for permanent environmental effects. The residual for the random regression includes the permanent environmental and residual variance together. Plotted for age 2, 3, and 4 yr.

LOSS calculated using random regression was lower than those calculated using multivariate (Table 5) analysis of BW and the BW change trait methods.

Additive, Phenotypic, and Heritability Estimates for BW gain

The additive variance for GAIN estimated using multivariate analysis was greater than that estimated using random regression (Table 6). As a consequence, the heritability estimated using random regression was lower than the heritability estimated with the multivariate analysis of BW and BW change trait analyses (Table 7). Additionally, GAIN became less heritable as ewes aged using all 3 methods. At age 2 yr, heritability of GAIN was greater compared with at age 3 yr and age 4 yr. The heritabilities for GAIN were always greater than LOSS.

Genetic Correlations between BW loss and BW gain

There was almost 0 genetic correlation between LOSS and GAIN except a medium negative correlation

Table 3. Akaike's information criterion (AIC) and the Bayesian-Schwarz information criterion (BIC) for multivariate and random regression analysis of BW at ages 2, 3, and 4 yr

Item	Age 2 yr	Age 3 yr	Age 4 yr
Log likelihood			
Multivariate	–12,836	–11,295	–8,675
Random regression	–12,862	–11,331	–8,679
AIC[1]			
Multivariate	25,713	22,630	17,389
Random regression	25,757	22,685	17,443
BIC[1]			
Multivariate	25,851	22,764	17,517
Random regression	25,875	22,799	17,552

[1]Low AIC and BIC values are preferred.

at age 3 yr when correlations were estimated with multivariate analysis of BW and the BW change trait (Table 8). At age 2 and 4 yr the genetic correlation between LOSS and GAIN was nearly 0 when estimated using the BW change trait and the multivariate analysis of BW (Table 8). Alternatively, these genetic correlations estimated using random regression were moderate and negative for age 2 and 4 yr. The genetic correlations between LOSS and GAIN for age 3 yr were greater than age 2 and 4 yr for all 3 methods. For ewes aged 3 yr, the genetic correlations estimated using BW change trait and multivariate analysis of BW were moderate and negative whereas the estimate using random regression analysis was very negative.

Genetic Correlations between Ages

The LOSS had low to moderate positive genetic correlations between ages (Table 9). The GAIN at age 2 yr. was moderately and positively correlated with GAIN at age 3 yr whereas BW gain at age 3 yr is the same trait as GAIN at age 4 yr. The correlations between LOSS at age 2 yr and LOSS at age 3 and 4 yr are moderate whereas correlation between ages 3 and 4 yr is low. This is not expected as ages 2 and 3 yr or ages 3 and 4 yr ought to have a greater genetic correlation than ages 2 and 4 yr although the SE are high for these correlations. The genetic correlations for the GAIN traits were more in line with expectations, with age 3 and 4 yr being highly correlated whereas there were lower correlations between age 2 and 3 yr as well as ages 3 and 4 yr. These results suggest that early growth to maturity at age 2 yr is different to growth in adult Merino during periods of high nutrient availability.

Table 4. Additive genetic [$\sigma^2_{a\,(WT2-WT1)}$] and residual plus permanent environmental [$\sigma^2_{e\,(WT2-WT1)}$] variance of BW loss (LOSS) calculated using the variance for each BW and covariance between BW estimated using multivariate analysis of BW and random regression analyses[1]

Additive genetic	$\sigma^2_{a\,WT1}$	$\sigma^2_{a\,WT2}$	cov_a(WT2,WT1)	$\sigma^2_{a\,(WT2-WT1)}$
Age = 2 yr				
Multivariate	17.7 (1.79)	15.5 (1.62)	16.2 (1.61)	0.89 (0.26)
Random regression	18.5 (1.73)	16.6 (1.65)	17.3 (1.68)	0.63 (0.23)
Age = 3 yr				
Multivariate	19.7 (2.74)	20.2 (2.50)	19.1 (2.50)	1.69 (0.56)
Random regression	20.5 (2.64)	19.7 (.46)	19.7 (2.49)	0.79 (0.48)
Age = 4 yr				
Multivariate	24.5 (3.64)	22.5 (3.13)	22.9 (3.21)	1.24 (0.65)
Random regression	23.2 (3.37)	22.1 (3.11)	22.4 (3.18)	0.42 (0.35)
Residual + permanent environmental	$\sigma^2_{e\,WT1}$	$\sigma^2_{e\,WT2}$	cov_e(WT2,WT1)	$\sigma^2_{e\,(WT2-WT1)}$
Age = 2 yr				
Multivariate	9.16 (1.17)	9.17 (1.08)	6.49 (1.05)	5.35 (0.28)
Random regression	8.74 (1.09)	8.54 (1.01)	5.83 (1.05)	5.62 (0.27)
Age = 3 yr				
Multivariate	20.5 (2.11)	14.0 (1.78)	12.6 (1.81)	9.24 (0.58)
Random regression	20.0 (2.09)	14.7 (1.72)	12.4 (1.77)	9.81 (0.54)
Age = 4 yr				
Multivariate	17.9 (2.75)	13.9 (2.30)	11.1 (2.34)	9.69 (0.72)
Random regression	19.4 (2.67)	14.6 (2.29)	11.8 (2.33)	10.3 (0.64)

[1]For example, the additive genetic variance was estimated using $\sigma^2_{a\,(WT2-WT1)} = \sigma^2_{a\,WT2} + \sigma^2_{a\,WT1} - 2 \times cov_a(WT2,WT1)$. Permanent environmental variance was only estimated for the random regression. Covariances cov_a and cov_e are additive genetic (a) and residual (e) covariances. WT1 = premating BW and WT2 = postmating BW.

DISCUSSION

Our study found that BW loss during periods of poor nutrition and BW gain during periods of good nutrition are genetically different traits. Additionally, BW loss and gain are genetically different in young ewes compared with old ewes. The estimates of heritability and correlations for BW change were different depending on the method used.

Table 5. Estimates of additive ($\sigma^2_{a\,LOSS}$) and phenotypic variance ($\sigma^2_{p\,LOSS}$) and heritability (h^2) for BW loss (LOSS) with SE (in parentheses) estimated using multivariate analysis of BW, random regression, and the BW change trait analyses

Method	Age[2]	$\sigma^2_{a\,LOSS}$	$\sigma^2_{p\,LOSS}$[1]	h^2
Multivariate	2	0.89 (0.26)	6.24 (0.20)	0.14 (0.04)
Random regression	2	0.63 (0.23)	6.06 (0.20)	0.10 (0.04)
BW change trait	2	0.86 (0.26)	6.24 (0.21)	0.14 (0.04)
Multivariate	3	1.69 (0.56)	10.9 (0.41)	0.15 (0.05)
Random regression	3	0.79 (0.48)	10.6 (0.40)	0.07 (0.03)
BW change trait	3	1.51 (0.55)	10.8 (0.41)	0.14 (0.05)
Multivariate	4	1.24 (0.65)	10.9 (0.47)	0.11 (0.06)
Random regression	4	0.42 (0.35)	10.7 (0.48)	0.04 (0.03)
BW change trait	4	1.23 (0.65)	10.9 (0.47)	0.11 (0.06)

[1]The phenotypic variance of LOSS was calculated by adding the additive, residual and permanent environmental variances from Table 4.

[2]Age measured in years.

Comparison of Methods

In this paper we used 3 methods for estimating genetic parameters. The estimates from the random regression analysis were clearly different from the estimates from the 2 other methods. The preferred method of the 3 is either the multivariate analysis of BW or BW change trait analyses because the multivariate analysis fit the data better than random regression according to the AIC and BIC. The BW change analysis cannot be directly compared with the multivariate and random regression analyses based on AIC and BIC but yields very similar results as the multivariate analyses. The random regression approach has a number of theoretical advantages but in our case was not an appropriate method. In our research, genetic correlations between BW at different time points were greater with random regression than with multivariate analysis of BW. This makes the heritability of BW change lower because there is less genetic variation in the difference between BW when they are highly correlated. This is different to the analysis by Huisman et al. (2002) who found that the correlations between 5 BW points in growing pigs had a similar correlation using both multivariate and random regression

Table 6. Additive genetic ($\sigma^2_{a\,(WT4-WT3)}$) and residual plus permanent environmental [$\sigma^2_{e\,(WT4-WT3)}$] variance of BW gain (GAIN) calculated using the variance for each BW and covariance between BW estimated using multivariate analysis of BW and random regression[1]

Additive genetic	$\sigma^2_{a\,WT3}$	$\sigma^2_{a\,WT4}$	cov_a(WT3,WT4)	$\sigma^2_{a\,(WT4-WT3)}$
Age = 2				
Multivariate	18.4 (1.81)	21.0 (2.59)	15.8 (1.88)	7.73 (1.31)
Random regression	15.9 (1.60)	19.9 (2.01)	16.0 (1.68)	3.62 (0.83)
Age = 3				
Multivariate	19.8 (2.48)	26.7 (3.67)	20.4 (2.67)	5.95 (1.55)
Random regression	19.6 (2.35)	23.5. (2.85)	20.3 (2.44)	2.63 (1.13)
Age = 4				
Multivariate	20.5 (3.27)	27.5 (4.42)	21.4 (3.38)	5.24 (1.78)
Random regression	21.8 (3.07)	24.5 (3.70)	21.2 (3.12)	3.87 (1.42)
Residual + permanent environmental	$\sigma^2_{e\,WT3}$	$\sigma^2_{e\,WT4}$	cov_e(WT3,WT4)	$\sigma^2_{e\,(WT4-WT3)}$
Age = 2				
Multivariate	9.08 (1.17)	19.9 (1.87)	6.61 (1.25)	15.8 (1.11)
Random regression	10.5 (1.08)	17.5 (1.78)	6.03 (1.09)	15.9 (1.09)
Age = 3				
Multivariate	14.9 (1.80)	24.5 (2.76)	8.78 (1.90)	21.9 (1.51)
Random regression	15.7 (1.60)	24.3 (2.51)	8.91 (1.71)	22.2 (1.51)
Age = 4				
Multivariate	19.3 (2.57)	26.5 (3.48)	11.0 (2.58)	23.8 (1.85)
Random regression	17.3 (2.33)	28.5 (3.14)	10.9 (2.32)	24.0 (1.86)

[1]For example, the additive genetic variance was estimated using $\sigma^2_{a\,(WT4-WT3)} = \sigma^2_{a\,WT4} + \sigma^2_{a\,WT3} - 2 \times cov_a(WT4,WT3)$. Permanent environmental variance was only estimated for the random regression. Covariances cov_a and cov_e are additive genetic (a) and residual (e) covariances. WT3 = prelambing BW; WT4 = weaning BW. Ages are in years.

analysis. With our data with only 4 BW points, multivariate analysis uses 20 parameters compared with the random regression, which uses 17, so there is not a major disadvantage for using the multivariate analysis whereas the multivariate analysis fits the data better than the random regression analysis.

Random regression could however be useful when data has more time points during the year because fewer parameters are required to predict variance and covariance using curves compared with multivariate analysis between many time points (Van der Werf et al., 1998). Additionally, if the measurements are recorded on different days for each individual making it harder to define specific traits or there are many missing values, random regression would be preferred. This is because multitrait models become over parameterized as the model tries to estimate variance and covariance for time points with

Table 7. Estimates of additive genetic ($\sigma^2_{a\,GAIN}$) and phenotypic variance ($\sigma^2_{p\,GAIN}$) and heritability (h^2) for BW gain (GAIN) with SE (in parentheses) estimated with multivariate analysis of BW, random regression, and the BW change trait methods

Method	Age, yr	$\sigma^2_{a\,GAIN}$	$\sigma^2_{p\,GAIN}$	h^2
Multivariate	2	7.73 (1.31)	23.5 (0.83)	0.33 (0.05)
Random regression	2	3.62 (0.83)	19.5 (1.24)	0.18 (0.04)
BW change trait	2	7.92 (1.32)	23.5 (0.84)	0.33 (0.05)
Multivariate	3	5.95 (1.55)	27.8 (1.05)	0.21 (0.05)
Random regression	3	2.63 (1.13)	24.9 (1.75)	0.11 (0.04)
BW change trait	3	4.89 (1.37)	27.6 (1.03)	0.18 (0.05)
Multivariate	4	5.24 (1.78)	29.1 (1.25)	0.18 (0.06)
Random regression	4	3.87 (1.42)	27.8 (2.1)	0.14 (0.05)
BW change trait	4	5.71 (1.68)	29.3 (1.26)	0.19 (0.05)

Table 8. Estimates of genetic correlations between BW loss (LOSS) and BW gain (GAIN; $r_{g\,LOSS\,GAIN}$) with SE in brackets estimated with multivariate analysis of BW, random regression and the BW change trait analyses

Method	Age, yr	cov(LOSS,GAIN)[1]	$r_{g\,LOSS\,GAIN}$
Multivariate	2	–0.00 (0.42)	–0.00 (0.16)
Random regression	2	–0.59 (0.25)	–0.47 (0.13)
BW change trait	2	0.08 (0.43)	0.03 (0.16)
Multivariate	3	–1.32 (0.66)	–0.42 (0.19)
Random regression	3	–1.27 (0.42)	–0.87 (0.21)
BW change trait	3	–1.33 (0.66)	–0.42 (0.20)
Multivariate	4	–0.09 (0.76)	–0.03 (0.30)
Random regression	4	–0.75 (0.50)	–0.57 (0.24)
BW change trait	4	–0.06 (0.75)	–0.02 (0.30)

[1]Estimated using $cov_a(WT2-WT1,WT4-WT3) = cov_a(WT1,WT3) + cov_a(WT2,WT4) - cov_a(WT1,WT4) - cov_a(WT2,WT3)$. Covariance cov_a is the additive genetic covariance. WT1 = premating BW; WT2 = postmating BW; WT3 = prelambing BW; WT4 = weaning BW.

Table 9. Genetic correlations between ages for BW loss (LOSS) and BW gain (GAIN; ±SE in parentheses)

	LOSS		GAIN	
Item	Age 3 yr	Age 4 yr	Age 3 yr	Age 4 yr
Age 2 yr	0.34 (0.24)	0.39 (0.30)	0.53 (0.14)	0.51 (0.15)
Age 3 yr		0.13 (0.32)		0.99 (0.15)

few records (Veerkamp et al., 2001). In our study however, the BW points were well clustered together making 4 distinct traits so there is no clear advantage of using random regression. Therefore, the multivariate analysis or the BW change analysis is preferred.

The multivariate analysis of BW change and the BW change trait were very similar in terms of heritabilities of BW change and the genetic correlations between loss and gain. The preferred method of the 2 is the multivariate analysis because fixed effects can be allocated to each BW separately. For example, the number of lambs born would affect weight at lambing more than at the start of mating. Therefore, the fixed effect of number of lambs born can be better modeled for each BW trait separately.

An important conclusion from our analysis is the difficulty in estimating variances and correlations between BW change traits. To estimate the correlation between LOSS and GAIN using multivariate and random regression, 4 estimated variances and 6 estimated covariances were used. Although the differences between the random regression and the multivariate estimates are not large in terms of model fit and variance components, differences in estimates accumulate in calculating genetic correlations between BW changes resulting in very different outcomes between random regression and multivariate analysis.

Heritability Estimates

Our analysis revealed that LOSS and GAIN are genetically different traits with LOSS less heritable than GAIN. This can be partly explained by the difference in periods over which GAIN and LOSS were calculated. The trait LOSS was BW change during mating on poor quality pasture and GAIN was BW change during lactation on good quality pasture. Therefore, the physiological process of the BW change would be different between the 2 periods. Also, GAIN was estimated from BW 131 d apart compared with the LOSS BW, which were 42 d apart. We did not divide BW change by the number of days of each period because there was little variation in number of days between animals for each period. Longer time between points allows bigger genetic differences to accumulate. Our study is in line with the previous studies showing that genetic variation exists in farmed animal populations to breed for increased tolerance against climate change (Ravagnolo and Misztal, 2000; Borg et al., 2009; Hayes et al., 2009; Rauw et al., 2010; Bloemhof et al., 2012).

Our estimates of heritability where different from other studies with Rauw et al. (2010) estimating greater heritability for BW loss and Borg et al. (2009) estimating a lower heritability. Also, Borg et al. (2009) estimated a lower heritability for BW gain. Both of these studies were done in a semiarid environment and used different breeds. Additionally, our heritabilities were estimated at each age independently, which makes a difference compared with pooling information from all ages together. For example, Vehviläinen et al. (2008) estimated lower heritability for survival with pooled generations compared with individual generations. Furthermore, we found genetic correlations between ages for LOSS and GAIN mostly less than 1. Therefore, LOSS and GAIN are not the same traits when ewes are maturing compared with when ewes are mature. The combination of different method, breed, environment, and timing of measurements may explain the different heritabilities between our study and the research by Borg et al. (2009) and Rauw et al. (2010).

Genetic Correlations between LOSS and GAIN

The genetic correlations suggest that LOSS and GAIN can be bred for independently and that LOSS and GAIN are different traits at different ages. There was close to 0 genetic correlation between LOSS and GAIN at ages 2 and 4 yr whereas there was a moderate negative (–0.42) correlation at age 3 yr when estimated with the multivariate analysis of BW and the BW change trait methods. Therefore, ewes can be selected to lose less BW potentially requiring less supplementary feeding and to gain more BW during spring and use more of the cheap feed supply, increasing their reserves before summer and autumn. The negative correlation at age 3 yr means that ewes that lose more BW also gain more BW, but the negative genetic correlation may have been due to sampling given the large standard errors.

Body weight loss appears to be lowly heritable at all ages, with little association across ages. Body weight gain appears to be moderately heritable, particularly among 2-yr-old ewes. The genetics of gain therefore resembles that of a growth trait. In contrast, loss behaves more like a physiological trait with less genetic variation. Body weight LOSS is genetically a different trait at different ages and is a different trait at age 2 yr compared with age 3 and 4 yr and GAIN at age 3 and 4 yr are genetically the same. This is probably because ewes at age 2 yr are still growing to mature size whereas ewes at age 3 and 4 yr are mature. Although GAIN is the same trait at age 3 and 4 yr, it is recommended to consider

LOSS and GAIN at different ages as different traits in genetic evaluation as well as in a selection index.

Implications for Breeding

The heritability estimates in this study show that it is feasible to breed adult Merino ewes that gain more BW. Body weight loss can also be selected for although the response to selection will be lower than for BW gain due to the lower heritability. Additionally, genetic correlations between LOSS and GAIN are mostly low, indicating that selection can be directed to 1 of them without affecting the other much. This means that sheep can be bred to lose less BW during periods of poor nutrition and gain more BW during periods of good nutrition. The implications of this depend on the role of BW change in the breeding goal and selection index of Merino sheep breeders.

Body weight change does not have a direct economic value in a selection index. However, it may be used in a selection index if it is genetically correlated to feed intake or efficiency. For example, BW loss could be used to represent breeding goal traits to reduce energy requirements for maintenance or increase intake when grazing poor quality feed (Silanikove, 2000; Fogarty et al., 2009). A study by Young et al. (2011a) calculated that reducing maintenance costs or increasing intake on poor pasture had a high economic value. The increase in profit was because farmers could manage more ewes on each hectare of land if they are more efficient. If ewes are, however, able to maintain or gain BW during summer due to reallocating resources from other competing body functions such as fertility or immunity (van der Waaij, 2004), then BW change does not represent efficiency within the breeding goal and is less valuable. Therefore, it will be useful to understand if ewes lose or gain more BW because they allocate their resources differently to wool, pregnancy, or lactation. This means that the genetic correlations between BW change and other production traits are needed before BW change can be used as an index trait.

Although all ewes had access to the same feed, the grazing behavior and actual intake by each ewe is not known. Therefore, it is possible that some ewes were more efficient at grazing or had first access to supplementary feed. To get better insight why some ewes lose less weight or gain more BW, individual feed intake data would be required.

Conclusion

In conclusion it is possible to breed adult ewes that lose less BW during periods of poor nutrition and gain BW during periods of good nutrition. More research is required to see if BW change can be used as an indicator trait for breeding goal traits such as feed intake or efficiency. If BW change is included in a breeding program, breeders need to consider the age of ewes and the timing of measurements. This research would benefit from a dataset with more measurements during the year that represents the trajectory of the BW curve better.

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